N94-30636

209943 P. 11

Models of Atmosphere-Ecosystem-Hydrology Interactions: Approaches and Testing

David S. Schimel

Introduction

Interactions among the atmosphere, terrestrial ecosystems, and hydrological cycle have been the subject of investigation for many years, although most of the research has had a regional focus (Hewlett and Hibbert, 1967; Wood et al., 1990). The topic is broad, including the effects of climate and hydrology on vegetation, the effects of vegetation on hydrology, the effects of the hydrological cycle on the atmosphere, and interactions of the cycles via material flux such as solutes and trace gases. The intent of this paper is to identify areas of critical uncertainty, discuss modeling approaches to resolving those problems, and then propose techniques for testing. I consider several interactions specifically to illustrate the range of problems. These areas are (1) cloud parameterizations and the land surface, (2) soil moisture, and (3) the terrestrial carbon cycle.

I separate the issues of process and scale somewhat artificially but for convenience in discussing the issues more clearly. Issues of process are those where biological or physical processes are not well understood. As an example, the biological controls over ecosystem response to CO₂ fertilization are not known, although hypotheses abound. Issues of scale are familiar in both the physical sciences, where considerable problems with cloud parameterizations persist, and biology, where the problem of extrapolating from the organism level (where our understanding is concentrated) to regions and the globe is unresolved. In some cases, the issues of process and scale become entangled. An example of this was presented in Jarvis and McNaughton's (1986) classic paper on scaling from leaf to canopy:

€

Ξ

Ξ

At some scale, transpiration becomes a control over itself by influencing boundary-layer humidity. This process, whereby the vegetation influences boundary-layer physics (Avissar and Verstraete, 1990), is one that only becomes apparent when the region of study achieves some critical size, and it is dependent upon the state of the atmosphere. Similarly, $\rm CO_2$ only becomes a control over climate (and hence terrestrial ecology) at the global scale, yet $\rm CO_2$ exchange is mediated by single leaves and microorganisms.

The interactions discussed in this chapter are not within subsystems of the earth system but at their interfaces (Moore, 1990), and the appropriate methods of validation are often unclear. For example, in ecological modeling, a strong test of a model is considered to be the comparison of model predictions to experimental data where the experiment is a manipulation of the system different from those used in developing the model. Another test would be to evaluate the model's ability to replicate system behavior along an environmental gradient (i.e., Parton et al., 1987). Clean application of these techniques for continental and global models is difficult; the biosphere does not have replicates, and replication is difficult even for landscape- to regional-scale simulations (Hobbs et al., in press). Bretherton (personal communication) uses the expression "increasing credibility" to refer to the process whereby models are incrementally challenged and improved in cases where full testing is impractical, as is the case with models of the coupled ocean-atmosphere-biosphere system. We must work continuously to challenge every testable part of the models so that they embody our best understanding. Critical to this is that feedbacks, once identified by experiment, by theory, or in the paleorecord, should be included and their significance evaluated. I will pursue these issues below, using the examples of cloud, soil moisture, and carbon cycle interactions. These interactions impose reciprocal constraints on model resolution and parameterization in both atmospheric and ecosystem/hydrological models, adding to their interest and challenge.

Cloud Feedbacks and Biology

It is well known now that cloud feedbacks are significant in the earth radiation budget (Ramanathan et al., 1989) and that clouds are poorly represented in current atmospheric general circulation models (GCMs) (Mitchell et al., 1989). While the effect of "cloud feedbacks" is often argued to be a negative feedback to global temperature (by reflecting radiation to space), it is less clearly understood that a change in cloudiness would in and of itself have a significant effect on plant energetics and physiology, possibly affecting primary

production and the outcome of plant competition. Several factors are involved in this plant-radiation interaction. First, photosynthesis (A) is highly and nonlinearly sensitive to incoming photosynthetically active radiation (PAR), with a response curve often fitted by a hyperbola (Johnson and Thornley, 1984).

Changes between cloud and clear sky radiation will have substantial effects on photosynthetic rates and associated evapotranspiration (ET). Because these rates are highly nonlinear, the parameterization chosen for clouds in a coupled atmosphere-biosphere model will have large consequences during climate change simulations. That is, taking a grid cell with humidity greater than threshold for cloud formation and assigning an average cloudiness will result in an average radiation field. Because the photosynthesis-PAR curve is strongly nonlinear, carbon and water exchange for that grid cell will be calculated incorrectly, possibly resulting in subsequent errors in the atmospheric water.

At steady state, this problem may be resolved by implicitly parameterizing the model to take into account "typical" cloud statistics, and this is often done. For nonsteady-state simulations or those of trace gas-modified climate, a physically based cloud statistic for each grid box is more desirable. The response of the vegetation can be correctly modeled by integrating the A-PAR function over the cloud distribution field for each grid cell.

The above argument assumes that the A-PAR relationship adjusts instantaneously and that PAR is the sole control over A. In fact, plant responses include lags and are controlled by multiple factors (Knapp and Smith, 1988; Schimel et al., 1991). First, while the drop in A following a decrease in PAR is rapid, the increase in A after PAR is increased may be slow (Knapp and Smith, 1990). Thus, an increase in cloudiness could produce a larger decrease in A and evapotranspiration than predicted with a linear extrapolation as a result of the hysteresis of the A-PAR relationship in time. This effect may be small at the global scale but has not been evaluated.

In water-stressed environments, cloudiness may actually increase net carbon gain. Water-stressed vegetation at high PAR will exhibit near-total stomatal closure and high resistance (g) to water and $\rm CO_2$ exchange. Thus in dry environments and under clear sky conditions, A may be near zero and ET low for much of the day, despite high photosynthetic capacity at full sunlight when well watered. Cloud passage under such conditions may allow stomatal opening and permit some photosynthesis. Knapp and Smith (1988, 1990) have shown that typical levels of cloudiness increase net daily A over that predicted for clear sky conditions in a subalpine environment.

Harman Markettan

::

This opens the following questions: (1) To what extent are such responses (hysteresis of A-PAR) tuned to the environment by evolutionary adaptation, or (2) how and how fast can plants respond to a changing light intensity? (3) Is the response physiological, in which case we may assume that a near-optimal response will keep pace with the changing environment, or (4) is the response genotypic, in which case the response will occur over time scales of community and evolutionary change (Field, 1990; Schimel et al., 1990).

In addition to the physiological processes, light also affects the outcome of competition between plant species. The widely used Jabowa family of models (e.g., Pastor and Post, 1986) includes the effects of light competition as a primary factor structuring forest communities. Each species included in the model has parameters describing its tolerance of high and low light levels, and shading is computed using a simple radiation model. While the response of ecosystem models to changing temperature and water has been evaluated (Schimel et al., 1990, 1991; Clark, this volume; Pastor and Post, 1988), effects of changing light environment have not been simulated. Indeed, scenarios of changing earth surface radiation from GCMs have not been widely released and may be quite unreliable (Smith and Vonder Haar, 1991). In fact, plant responses to the absolute light environment (as opposed to the relative light environment defined by shading) may not be well known.

Returning to the issue of cloud parameterizations in atmospheric GCMs (AGCMs), it is clear that simulated cloudiness structure or statistics in the AGCM not only must satisfy the requirements of correct simulation of the cloud radiation feedback on mean global and regional temperature. It also must accurately model the variability of clouds and hence the solar radiation field at the earth's surface for correct simulation of plant response. The time scales of these two requirements may well be different. For example, the earth radiation budget is normally calculated with a time step of about a month, and radiation calculations in most AGCMs are integrated at longer time steps than many other processes. For simulation of A, ET, and g, statistics describing the variability in monthly cloudiness but for morning, midday, and afternoon conditions may be required. Cloud parameterizations in AGCMs should be developed with requirements based on sensitivity analyses of ecosystem models as one criterion. In addition, the use of cloud statistics in ecosystem simulations should be investigated further.

One type of model subsystem checking is conceptual checking to insure that no important process has been omitted. The above discussion points out a series of interactions that have not been considered in the development of most models of land surface interac-

Ē.

tions. Assuming that the above interactions were to be included in an earth system model, how could they be tested? This question has a number of answers. First, the physiological response of plants to cloudiness can be investigated using leaf and canopy measures of gas exchange, and some such studies are under way (Knapp, personal communication; Knapp and Smith, 1988, 1990). In addition, many data sets collected using eddy correlation measurements of water and CO₂ exchange include incoming radiation or even cloud statistics (e.g., the first ISLSCP [International Satellite Land Surface Climatology Program] Field Experiment [FIFE] Information System, NASA-Goddard Space Flight Center) and could be analyzed for effects of cloudiness and hysteresis. Cloud passage is often treated as a noise term but could be analyzed as a signal.

The physiological adaptation of plants to new cloud regimes could be simulated experimentally using growth facilities or transplants but will be difficult to relate to the field situation and to global change. The effects of changing light environment on plant competition can be modeled using improvements of extant models but will be well-nigh impossible to test in the field given the time scale of plant succession. In this area, sensitivity analysis of rigorously developed models may have to suffice, possibly augmented with field studies using analogous gradients.

Soil Moisture

Soil moisture is a key parameter linking atmosphere and biosphere. Soil moisture is a key control over decomposition (Parton et al., 1987), over leaching of nutrients, and over plant growth. The central role of soil moisture storage and of runoff to the biota and hydrology make their correct representation in earth system models crucial. In order to simulate the surface energy balance, climate models use the basic prognostic equation for soil moisture (w):

$$\frac{\partial(\mathbf{w})}{\partial t} = \mathbf{r} - \mathbf{E}\mathbf{T} + \mathbf{m} - \mathbf{f} \tag{1}$$

where r is rainfall, ET is evapotranspiration, m is snowmelt, and f is runoff. Recent work has focused on improving the representation of ET (Sellers et al., 1986). This approach is acceptable for simulation of sensible and latent heat exchange over broad areas, but is it adequate for linking climate, plant growth, and biogeochemistry?

There are several issues to consider. First, plant available water (pw) is defined by the following equation in real landscapes:

$$\frac{\partial(pw)}{\partial t} = f_{t,om}[r - ET + m - f + i - d]$$
 (2)

Ξ

ij

where pw is plant available water; t is time; om is organic matter content; r, ET, m, and f are as above; d is deep drainage; and i is run-on. The function must be converted from total water (the conserved quantity) to plant available water using the soil moisture release function, which varies largely as a function of soil texture and soil organic matter content. In many ecosystems, run-on is a significant control over landscape-scale plant production as much of the production may be concentrated in zones of run-on (Schimel et al., 1985; Noy-Meir, 1977). Similarly, trace gas efflux may be much greater from zones of water concentration than from upland areas (Schimel et al., 1985; Parton et al., 1988), both because of higher microbial activity and because of the erosional concentration of nutrients in run-on zones (Schimel et al., 1986).

The above issues raise problems of scale. The simple prognostic equation for soil water, as modified to include detailed representation of evapotranspiration, currently suffices to simulate atmospheric moisture and surface energy balance in AGCMs. These representations may also suffice for calculations of water balance for large drainages (Gleick, 1987). When the focus of interest changes to the biosphere, these representations become less satisfactory. Stored soil water is an influence over plant production in many ecosystems, and this is of course influenced by position in the runoff/run-on continuum. Field studies and simulations of nitrous oxide (N_2O) and ammonia (NH_3) flux show position in the landscape along this continuum to be of predominant importance (Schimel et al., 1986; Parton et al., 1988). Similarly, methane flux is influenced by meso- and microscale hydrology and topography (Whalen and Reeburgh, 1988). The above problems require mapped or statistical data on topography, soil properties, vegetation, land use, and engineering structures for resolution in models. Clearly, some of these problems require resolution higher than achievable or desirable in an earth system model; equally clearly, these processes (productivity, trace gas flux) are of significance to the earth system.

Improved coupling of atmospheric and hydrological models is also important to understanding the interactive role of fresh water ecosystems in the earth system. Changes in climate will have significant consequences for rivers and lakes, and these changes will undoubtedly have feedbacks, at least to regional climate and certainly to human societies. Current AGCMs include no representation of fresh water interactions and barely even include them due to coarse resolution of geography. Yet fresh water systems are critical to nutrient and organic matter transport, interact strongly with marginal wetlands, and are the dominant vector for nutrient transport to the oceans. There have been repeated critiques of the lack of

consideration of coastal and shelf regions of the oceans in global carbon cycle models; simulation of these areas will require consideration of the inputs from fresh water systems. Indeed, as Broecker (1981) has pointed out, fresh water may play a dominant role in millennial changes in ocean circulation and climate.

A critical link in the land surface-atmosphere-hydrology part of the "wiring diagram" then is the interface between global and regional changes in P-E, and their expression in real hydrological systems. A variety of approaches has been used to develop such interfaces. Wilks (1988) used a statistical conversion from AGCMpredicted changes to "real" weather and soil properties from a crude data base to translate between AGCMs and detailed plant models but did not address run-on/runoff and other landscape processes. Schimel et al. (1990) used a similar approach for biogeochemical cycling. Gleick (1987) used AGCM output as input to a basin hydrology model, but focused on water output rather than on distribution and effects within a watershed. Giorgi (1990) used a mesoscale atmospheric model forced by AGCM output and a land surface parameterization to examine effects of mountainous topography and sub-AGCM grid circulations; this study did not consider routing of runoff. Vörösmarty et al. (1989) used a basin-scale hydrological model to study the routing of runoff within a large drainage (the Amazon) and its effects on evapotranspiration and nutrient flux. This model could be forced by simulations such as those of Dickinson (1987) or Shukla et al. (1990) to evaluate regional hydrological consequences of a changed vegetation in the Amazon region.

The problems of including hydrology in earth system models are serious, however. Wood et al. (1990) have pointed out that most hydrological models are extensively parameterized to account for the peculiar features of topography, soils, and geology in a catchment area of interest. This is because of the complex nonlinear interactions that occur within catchments, and the detailed geographic data required to analyze those interactions. The response of catchments is also very sensitive to initial conditions (Wood et al., 1990; Figure 1), again resulting in complex responses. Work by Wood, Band, Gupta, and others (Wood et al., 1990; Wood et al., 1988; Gupta et al., 1986; Band and Wood, 1988) has attempted to develop scale-independent measures that can be used to develop simplified models of watershed response, at least above threshold sizes (Representative Elementary Areas: Wood et al., 1990). These theoretical approaches and simulations hold promise for developing improved representation of land surface hydrology and its interactions with biology and the atmosphere in the near future. Improvement of the representation of hydrology in earth system models will greatly aid

а

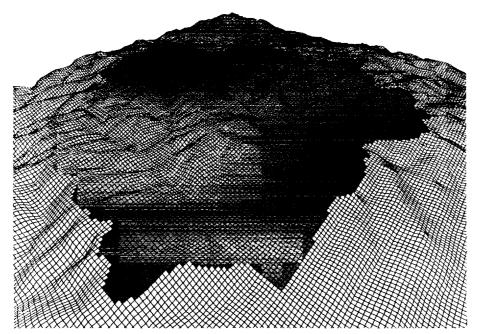


Figure 1. Results of simulations of runoff on a Kansas tallgrass prairie water-shed (Konza Prairie Research Natural Area Long-Term Ecological Research Site; also, the site of FIFE. Adapted from Wood et al., 1990). Patterns are superimposed on the digital elevation model of the site. (a) Rainfall for a storm on August 4, 1987; (b) predicted runoff assuming dry initial conditions.

in improving the biogeochemistry and biology in these models, but improvements to the runoff routing will be required in addition to improved ET simulations.

Validation of earth system models including hydrology is again difficult. Replication is essentially impossible at the scales of interest and experimental manipulation unlikely. Two approaches have been used with some success. The large field experiment, exemplified by FIFE or the Hydrological Atmospheric Pilot Experiment (Sellers et al., 1988), can test parameterizations of the ET and small-scale routing issues by extensive measurements of soil moisture, stream flow, and fluxes above the canopy. Basin-scale investigations can compare model simulations to river hydrographs (Vörösmarty et al., 1989), although the validity of the internal processes remains untested. In the end, these models will have to be tested against a few intensive field studies and long-term records and then compared broadly to routinely collected data on rainfall, stream and river flow, and river biogeochemistry. Simulations of paleoevents, such as the

6

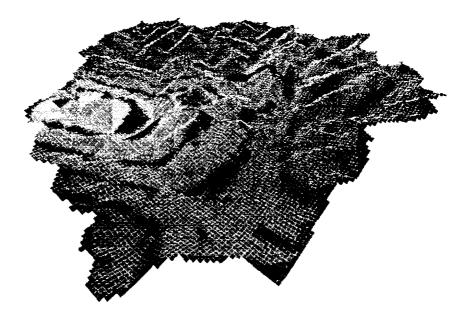


Figure 1(b).

hypothesised Younger Dryas event, will also be helpful in establishing confidence in these complex simulations. Finally, the global parameterizations should be based on extensively tested and more complex regional models.

The Carbon Cycle

Issues in the terrestrial carbon cycle have been extensively argued over the past decade or so, and many unresolved questions remain (Houghton et al., 1983; Detwiler and Hall, 1988; Tans et al., 1990). Tremendous effort has been expended on resolving the question of whether the terrestrial biosphere is a source or sink for CO_2 . I will not attempt a new analysis of this question but will instead outline steps that seem necessary to resolving it, and further steps required for inclusion of an interactive terrestrial biosphere in earth system models. The questions that must be answered to address the source/sink issue seem now to be: (1) Where and when, if ever, is

CO₂ fertilization expressed? (2) What are the geography and carbon budgets for disturbed ecosystems; can these systems be a sink? (3) Can climate change (variability) over the past century have caused a directional change in carbon storage? In order to include an interactive biosphere into earth system models, the following additional questions must be answered: (1) If terrestrial ecosystems are now a sink, what are the limits to sink strength? (2) How will vegetation distribution change and how will this affect the carbon cycle? Finally, for both issues (source/sink, predictive models), how can the answers be tested at large scales?

Can the terrestrial biosphere serve as a long-term sink for carbon? Enhanced CO_2 will lead to increased photosynthesis under certain conditions. Three factors may limit the significance of this increase. First, it may be a transient, as some evidence shows that plants may acclimate to increased CO_2 and show a gradually decreasing response.

Second, the effects of CO_2 may be attenuated by constraints from other limiting factors. Nutrients or water may limit CO_2 uptake at levels only slightly greater than under current CO2 concentrations. The interaction of CO_2 fertilization with other limiting factors requires far more study in a range of ecosystems with varying limiting factors. CO2 fertilization has the potential to alter nitrogen and water use by allowing increased enzyme efficiencies (photosynthetic enzymes contain large amounts of N) or by increasing water-use efficiency through stomatal effects. Under most circumstances, these changes in wateror N-use efficiencies will result in the production of plant tissue with reduced content of N and other nutrients. This is because CO2 fertilization does not enhance nutrient availability through any known mechanism and, with increased efficiency, more biomass will be produced on the same amount of nutrients. The production of plant tissue with higher C:element ratios will increase microbial uptake of nutrient when that tissue is decomposed, competing with plants and reducing nutrient availability (Parton et al., 1987; Melillo et al., 1984). This feedback will tend to reduce the effects of CO₂ fertilization on primary production, homeostatically. We have evaluated the consequences of increasing CO2 on carbon storage in a grassland model (Figure 2) and found the behavior described above to apply; that is, feedback through plant-microbial competition for nutrients limited the effects of CO_2 -induced increases in resource use efficiencies.

Third, an extrapolation of the above effect suggests that the ability of terrestrial ecosystems to store carbon is limited by the availability of other resources. If CO_2 were to increase carbon storage in some or most ecosystems, how much carbon could they store? A certain amount of C can be stored in plant biomass, especially in

wood. However, the maximum biomass of forests is constrained mechanically, by nutrients and light, and by human requirements for forest products. Carbon storage in soil organic matter is a more permanent sink, having a turnover time of hundreds to thousands of years. All organic matter, however, has nutrients associated with it, and soil organic matter is normally quite rich in nutrients. For example, N in humus is generally 5 to 20 times more concentrated than in plant biomass (Parton et al., 1987). Thus any major increase in soil carbon will constitute a major sink for N and other nutrients, eventually leading to the same sorts of restrictions on primary productivity described above. In effect, the humus becomes a competitive sink for nutrients with the plants, and production must decline. Bogs and other wetland areas where peat accumulates are the contemporary examples of this process, having high carbon storage and low primary productivity.

The use of fertilization in agriculture to support or enhance the direct CO_2 effects on primary production would seem to enhance a negative feedback to atmospheric CO_2 concentration. However, rates of decomposition are relatively high in agricultural systems and rates of carbon stabilization low. Most agricultural soils contain at the most a few percent carbon, and the carbon content tends to decline slowly or stabilize at low levels (Bouwman, 1990). Thus the negative feedback due to fertilizing agricultural soils is limited; however, carbon once stabilized in cultivated soils may have a long residence time (Parton et al., 1987; Trumbore et al., 1990).

Disturbed ecosystems may pass through a period of rapid carbon accumulation, where stocks of biomass and soil carbon are replenished (see Houghton et al., 1983). This phenomenon is evident in recently harvested forests, after burning, and following severe storm damage. The expansion of the use of terrestrial ecosystems in the past century may have "reset the clock" for many ecosystems to the point where they are accumulating organic matter rapidly and serving as a sink. While the accumulation of carbon following disturbance is included explicitly in the budgetary estimates of Houghton et al. (1983) and Detwiler and Hall (1988), our data on the geography of disturbance and recovery rates are not numerous (Botkin and Simpson, 1990).

In conclusion, terrestrial ecosystems are unlikely to be a long-term sink for CO_2 , although certain areas act as sinks for some intervals. The ability of ecosystems to store carbon is limited and unlikely to accommodate the extent of atmospheric CO_2 increases projected as a consequence of industrial civilization.

If greenhouse gas emissions lead to increased temperatures, this will also affect the carbon cycle. Increased temperatures, other fac-

tors being equal, will accelerate decomposition and cause loss of stored carbon, increasing the atmospheric inputs of CO2 (Schimel et al., 1990). In general, decomposition is quite sensitive to temperature (e.g., Parton et al., 1987). In a recent simulation exercise, we showed that across a range of grasslands, increased temperature resulted in soil carbon losses despite enhanced production due to CO₂ enrichment (Figure 2). While this result is only for one ecosystem type, other models exhibit similar behavior for other ecosystem types (Pastor and Post, 1986), suggesting it may be a fairly general result. If this is true, then CO2 fertilization responses may not keep pace with respiration losses resulting from increases in temperature. It is also possible that climate changes over the past few centuries, including a possible greenhouse effect term, have resulted in significant changes in soil carbon storage. Substantial improvements in data and models will be required to test this hypothesis and even to establish the direction of the change; nonetheless, this would be an interesting exercise even with current process models.

Testing process-based models of the carbon cycle presents major challenges. While regional models can be developed and tested effectively, repeating this process in every ecosystem globally is precluded by logistics. Testing at the global scale is feasible using atmospheric $\rm CO_2$ concentration gradients, but these tests do not test the internal dynamics of the model very well, and hence the predictive capability of the model remains in question.

Ē

I suggest a strategy based on three techniques. First, models should be based on understanding of principles that have been proven to be broadly applicable—a theory-based approach—rather than on empirical relationships (Schimel et al., in press). Real progress is being made in this area for both autotrophic and heterotrophic processes, although empirical models remain the dominant type for global representations.

Second, while traditional field tests cannot be made everywhere, remote sensing can obtain data in virtually all terrestrial ecosystems. Remote observations can serve to quantify temporal and spatial distributions of ecosystem properties with current techniques (Tucker et al., 1986). Excellent progress is being made on retrieving more quantitative information on hydrology, physiology, and biogeochemistry using satellite data (Schimel et al., 1991b; Wessman et al., 1988). While many of the traditional formulations for ecological and hydrological processes are not readily tested with remote sensing, often these models may be transformed or reparameterized to allow such testing (Schimel et al., 1991b).

Finally, the aggregate output of models already tested regionally using remote sensing and field techniques can be compared to

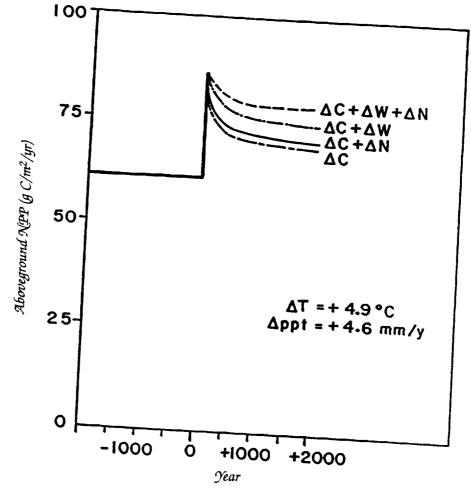


Figure 2. Century simulations showing the response to changing water-use efficiency (ΔW), nitrogen-use efficiency (ΔN), and both to simulate the direct effects of CO_2 enrichment (ΔC). The altered water-use efficiency and nitrogen-use efficiency were imposed after a step change in temperature and precipitation to a doubled- CO_2 climate. Note that despite enhanced NPP, the net effect of the temperature increase was a reduction in stored carbon due to increased decomposition.

atmospheric CO_2 and other trace gas fields. Comparison of predicted source/sink relationships may be compared to inverse calculations of those sources and sinks (Tans et al., 1990).

In summary, while no one method of testing will allow full confidence to be established in carbon biogeochemistry models, the application of a hierarchy of tests will allow comprehensive evaluation. Application of the tests proposed is contingent on continued development of theory and practice for both ecosystem analysis and

Ξ

measurement techniques, especially remote sensing. Progress in these areas is very encouraging although major challenges remain.

Conclusions

Interactions of the terrestrial biosphere and hydrology with the atmosphere are a critical component of earth system modeling; these interactions will influence the trajectory both of climate, especially regional climate, and of ecosystems upon which humankind depends for sustenance. Critical gaps remain in the modeling of these interactions. In many cases these gaps arise because of the independent evolution of atmospheric, hydrological, and ecological models within those disciplines. Because of this independent evolution, connections and reciprocal requirements must now be worked out as earth system modeling emerges as a major research area.

References

- Avissar, R., and M.M. Verstraete. 1990. The representation of continental surface processes in atmospheric models. Reviews of Geophysics 28, 35-52.
- Band, L., and E.F. Wood. 1988. Strategies for large scale distributed hydrological simulation. Applied Mathematics and Computation 27, 23-37.
- Botkin, D.B., and L.G. Simpson. 1990. Biomass of the North American boreal forest: A step toward accurate global measures. Biogeochemistry 9, 161-174.
- Bouwman, A.F. 1990. Background. In Soils and the Greenhouse Effect (A.F. Bouwman, ed.), John Wiley and Sons, New York, 25-167.
- Broecker, W.S. 1981. Glacial to interglacial changes in ocean and atmospheric chemistry. In Climate Variations and Variability: Facts and Theories (A. Berger, ed.), D. Reidel, Dordrecht, The Netherlands, 109-120.
- Detwiler, R.P., and C.A.S. Hall. 1988. Tropical forests and the global carbon cycle. Science 239, 42-47.
- Dickinson, R.E. (ed.) 1987. The Geophysiology of Amazonta. John Wiley and Sons, New York.
- Field, C.B. 1990. Ecological scaling of carbon gain to stress and resources availability. In Integrated Response of Plants to Stress (H.A. Mooney, W.E. Winner, and E.J. Pell, eds.), Academic Press, New York.
- Giorgi, F. 1990. Simulation of regional climate using a limited area model nested in a general circulation model. Journal of Climate 3, 941-963.

- Gleick, P.H. 1987. Regional hydrological consequences of increases in atmospheric ${\rm CO_2}$ and other trace gases. Climatic Change 10, 137–160.
- Gupta, V., I. Rodrigues-Iturbe, and E.F. Wood. 1986. Scale Problems in Hydrology. D. Reidel, Hingham, Massachusetts.
- Hewlett, J.D., and A.R. Hibbert. 1967. Factors affecting the response of small watersheds to precipitation in humid areas. In Forest Hydrology (W.E. Sopper and H.W. Lull, eds.), Pergamon, New York.
- Hobbs, N.T., D.S. Schimel, D.S. Ojima, and C.E. Owensby. Environmental contingency influences ecosystem processes: Fire and grazing in the tallgrass prairie. *Ecology*. in press.
- Houghton, R.A., J.E. Hobbie, J.M. Melillo, B. Moore III, B.M. Peterson, G.R. Shaver, and G.M. Woodwell. 1983. Changes in the carbon content of terrestrial biota and soils between 1860 and 1980. Ecological Monographs 53, 235–262.
- Jarvis, P.G., and K.G. McNaughton. 1986. Stomatal control of transpiration: Scaling from leaf to region. Advances in Ecological Research 15, 1-49.
- Johnson, I.R., and J.H.M. Thornley. 1984. A model of instantaneous and daily canopy photosynthesis. *Journal of Theoretical Biology* 107, 531-545.
- Knapp, A.K., and W.K. Smith. 1988. Effects of water stress on stomatal and photosynthetic responses in subalpine plants to cloud patterns. American Journal of Botany 75, 851–858.
- Knapp, A.K., and W.K. Smith. 1990. Stomatal and photosynthetic responses to variable sunlight. *Physiology Plantarum* 78, 160–165.
- Melillo, J.M., R.J. Naiman, J.D. Aber, and A.E. Linkins. 1984. Factors controlling mass loss and nitrogen dynamics of plant litter decaying in northern streams. *Bulletin of Marine Science* 35, 341–356.
- Mitchell, J.F.B., C.A. Senior, and W.J. Ingram. 1989. CO₂ and climate: A missing feedback? *Nature 341*, 132–134.
- Moore, B. 1990. Committee on Global Change (U.S. National Committee for the IGBP). Integrated modeling of the earth system. In *Research* Strategies for the U.S. Global Change Research Program, National Academy Press, Washington, D.C., 1990, 67-107.
- Noy-Meir, I. 1977. Desert ecosystems: Environment and producers. *Annual Review of Ecology and Systematics* 4, 23–51.
- Parton W.J., A.R. Mosier, and D.S. Schimel. 1988. Rates and pathways of nitrous oxide production in a shortgrass steppe. *Biogeochemistry* 6, 45–58.

Î

The Landson and

199

=

主量

- Parton, W.J., D.S. Schimel, C.V. Cole, and D.S. Ojima. 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. Soil Science Society of America Journal 51, 1173–1179.
- Pastor J., and W.M. Post. 1986. Influence of climate, soil moisture and succession on forest carbon and nitrogen cycles. *Biogeochemistry* 2, 3-27.
- Pastor, J., and W.M. Post. 1988. Response of northern forests to CO₂-induced climate change. *Nature 334*, 55–58.
- Ramanathan, V., B.R. Barkstrom, and E.F. Harrison. 1989. Clouds and the earth's radiation budget. *Physics Today* 42, 22–32.
- Schimel, D.S., M.A. Stillwell, and R.G. Woodmansee. 1985. Biogeochemistry of C, N and P in a soil catena of the shortgrass steppe. *Ecology 66*, 276–282.
- Schimel, D.S., W.J. Parton, F.J. Adamsen, R.L. Senft, and M.A. Stillwell. 1986. The role of cattle in the volatile loss of nitrogen from short-grass steppe. *Biogeochemistry* 2, 39–52.
- Schimel, D.S., W.J. Parton, T.G.F. Kittel, D.S. Ojima, and C.V. Cole. 1990. Grassland biogeochemistry: Links to atmospheric processes. *Climatic Change* 17, 13–25.
- Schimel, D.S, T.G.F. Kittel, A.K. Knapp, T.R. Seastedt, W.J. Parton, and V.B. Brown. 1991a. Physiological interactions along resources gradients in a tallgrass prairie. *Ecology* 72, 672–684.
- Schimel, D.S., T.G.F. Kittel, and W.J. Parton. 1991b. Terrestrial biogeochemical cycles: Global interactions with the atmosphere and hydrology. *Tellus* 43(4), 188–203.
- Sellers, P.J., Y. Mintz, C. Sud, and A. Dalcher. 1986. A simple biosphere (SiB) model for use within general circulation models. *Journal of the Atmospheric Sciences* 43, 505–531.
- Sellers, P.J., F.G. Hall, G. Asrar, D.E. Strebel, and R.E. Murphy. 1988. The First ISLSCP Field Experiment (FIFE). Bulletin of the American Meteorological Society 69, 22–27/
- Shukla, J., C. Nobre, and P.J. Sellers. 1990. Amazonian deforestation and climate change. *Science* 247, 1322–1325.
- Smith, L.D., and T.H. Vonder Haar. 1991. Clouds-radiation interactions in a general circulation model: Impact upon the planetary radiation balance. *Journal of Geophysical Research 96*, 893–914.
- Tans, P.P., I.Y. Fung, and T. Takahashi. 1990. Observational constraints on the global atmospheric CO_2 budget. Science 247, 1431–1438.

- Trumbore S.E., G. Bonani, and W. Wolfli. 1990. The rates of carbon cycling in several soils from AMS ¹⁴C measurements of fractionated organic matter. In *Soils and the Greenhouse Effect* (A.F. Bouwman, ed.), John Wiley and Sons, New York, 407–414.
- Tucker, C.J., I.Y. Fung, C.D. Keeling, and R.H. Gammon. 1986. Relationship between atmospheric CO₂ variations and a satellite-derived vegetation index. *Nature 319*, 195–199.
- Vörösmarty, C.J., B. Moore III, A.L. Grace, M.P. Gildea, J.E. Melillo, B.J. Peterson, E.B. Rastetter, and P.A. Steudler. 1989. Continental-scale models of water balance and fluvial transport: An application to South America. *Global Biogeochemical Cycles* 3, 241–265.
- Wessman, C.A., J.D. Aber, D.L. Peterson, and J.M. Melillo. 1988. Remote Sensing of canopy chemistry and nitrogen cycling in temperate forest ecosystems. *Nature* 335, 154–156.
- Whalen, S.C., and W.S. Reeburgh. 1988. A methane flux time series for tundra environments. *Global Biogeochemical Cycles* 2(4), 399–409.
- Wilks, D. 1988. Estimating the consequences of CO_2 -induced climatic change on North American grain agriculture using general circulation model information. *Climatic Change* 13, 19–42.
- Wood, E.F., M. Sivapalan, K. Beven, and L. Band. 1988. Effects of spatial variability and scale with implications to hydrological modeling. Journal of Hydrology 102, 29–47.
- Wood, E.F., M. Sivapalan, and K. Beven. 1990. Similarity and scale in catchment storm response. *Reviews of Geophysics* 28, 1–18.

,			
\$ \$			
•			
÷			
-			
=			
= = - =			
-			
-			
į			
4			
Ī			
4			
-			
1			
an opperation of the control of the			
_			
-			
-			
- -			
Ē			
Ē			
Ē			
÷			
Ē			
÷			
÷			
÷			
÷			

-

and a second of the second of

Ξ -